**VERTEBRATE**

By the beginning of the Cambrian, 540 million years ago, a great variety of animals inhabited the earth’s oceans.

* Claws, mandible, protective plates and spikes, complex mouth parts, teeth, skeletons, limbs.
* Hard parts and skeletons appeared that initiated changes in the location and attachment of tissues. These hard parts provided protection, support and teeth (for predators).

Vertebrates remain restricted to the oceans for nearly 200 million years until Devonian (360 m.y.a.).

By the Devonian, 360 m.y.a., the transition to land took place.

Deuterostomes have two main branches, Echinodermata and Chordata.

The phylum Chordata is divided into three subphyla:

1. Subphylum Urochordata
2. Subphylum Cephalochordata
3. Subphylum Vertebrata

**PHYLUM CHORDATA**

Chordates are coelomate animals with bilateral symmetry, segmented body, with a tube-within-a-tube body plan and three well-developed germ layers, an endoskeleton and closed circulatory system. About 42,000 species known so far.

**DERIVED CHARACTERS OF CHORDATES**

All chordates share a set of derived characters, though many species possess some of these traits only during embryonic development.

DISTINGUISHING CHARACTERISTICS

1. **Notochord**.

* Cartilaginous rod running underneath and supporting the nerve cord. It is located between the nerve cord and the digestive tube.
* Made of large, fluid-filled cells surrounded by stiff, fibrous tissue.
* Provides flexible support and a place for muscle attachment in those organisms that retain it.
* It persists in the adult of some invertebrate chordates and primitive vertebrates.
* Replaced by vertebrae in the adults of many groups. The gelatinous material of the disks between the vertebrae in humans is the remnant of the notochord.

1. **Dorsal nerve cord**.

* Single, hollow, dorsal cord above the notochord.
* Develops from a plate of ectoderm that rolls into a tube dorsal to the notochord.
* It becomes the central nervous system: brain and spinal cord.
* Other animals have a solid cord located on the ventral side of the body.

1. **Pharyngeal slits**.

* Present in the embryo and adult of some species.
* In all chordate embryos a series of pouches separated by grooves forms along the sides of the pharynx.
* Function as suspension-feeding devices in many invertebrate chordates.
* The slits and structures supporting them have become modified for gas exchange, jaw support, hearing, and other functions during vertebrate evolution.

1. **Muscular post-anal tail**.

* Prominent in embryos of all groups but not in all adults.
* The chordate tail contains muscle and skeletal elements, and provides most of the propelling force in many aquatic species.

**INVERTEBRATE CHORDATES**

**1. UROCHORDATES (tunicates)**

* Urochordates are commonly known as **tunicates**. The animal is covered with a cellulose-like carbohydrate.
* Larval stage is chordate with gills, notochord and dorsal nerve cord.
* These structures are lost in the adult stage except for the gill slits, which are present in the adult. It undergoes a radical metamorphosis.
* Adults are sessile marine organisms; develop a protective covering or tunic with siphons.
* Water enters the incurrent siphon, passes through the pharyngeal slits, into a chamber called the atrium, and exits through a excurrent siphon or atriopore.
* Suspension feeders. Food is trapped by a mucous net and transported by cilia to the esophagus. The anus opens into the excurrent siphon.
* Some species are colonial in which members share a common tunic and excurrent siphon.
* Colonial forms usually reproduce asexually by budding; sexual forms are commonly hermaphroditic.

<http://www.biology.ucok.edu/AnimalBiology/Chordata/Urochordata.html>

**2. CEPHALOCHORDATES (lancelets)**

Share with the Vertebrata the following characteristics:

* Notochord, gill slits, dorsal nerve cord, metameric muscles (<<<<), posterior direction of blood flow in the dorsal vessel and anterior blood flow in the ventral vessel, thyroid, homologous homeobox gene clusters. Larva similar to the Agnatha.
* Notochord extends to the anterior end (cephalochordates!) and does not end at a brain.
* Adults are suspension feeders burrowing in the sea bottom. A mucous net covering the pharyngeal slits removes tiny food particles from seawater drawn into the mouth by ciliary movement.
* Gas exchange occurs through the skin.
* Muscles arranged in a serial row of chevrons (<<<<<). They develop from sections of mesoderm called **somites**. Arranged along each side of the notochord.
* Example: Branchiostoma (= Amphioxus), lancelet.

<http://www.biology.ucok.edu/AnimalBiology/Chordata/Cephalochordata.html>

**EARLY CHORDATE EVOLUTION**

**Paedogenesis hypothesis of the origin of vertebrates.**

Garstang proposed in the 1920s the **paedogenesis hypothesis** in an attempt to explain early chordate evolution.

According to this theory, an ancestral cephalochordate evolved from a larva of a urochordate through a process of paedogenesis in which a larva becomes sexually mature.

* Changes in genes controlling the time of development could alter the moment of gonad maturation. This could have created a sexually mature larva before metamorphosis into the sessile form.
* If this process was successful, natural selection would have favored paedogenesis and eliminate metamorphosis.

This hypothesis is now discarded base on studies that suggest that tunicate adult and larva are highly derived.

Studies of *Hox* genes expression suggest that the tunicate larva does not develop the posterior regions of its body axis. The anterior region is elongated and contains a heart and digestive system.

The lancelet brain consists of a small cluster of cells forming a swollen tip at the apex of the nerve cord.

Study of the *Hox* genes that control the development of the vertebrate brain have shown that the same sequence of expression occurs in the lancelet.

It appears that the vertebrate brain is an elaboration of an ancestral structure similar to the lancelet’s simple nerve cord tip.

Chordates with heads are known as **craniates**.

The head contains the brain at the anterior end of the nerve cord and contains sense organs like eyes and hearing devices; these structures are surrounded by a skull.

The development of the head allows now **active predation**, a new way of feeding.

**DERIVED CHARACTERS OF THE CRANIATES**

The following characteristics distinguish craniates from other chordates. All craniates share these characteristics.

DISTINGUISHING CHARACTERISTICS

1. Craniates have **two clusters of Hox genes**; urochordates and cephalochordates have only one cluster of Hox genes.
   * Other families of genes that produce certain transcription factors are also duplicated in the craniates.

* This genetic duplication is interpreted as allowing the development of a more complex morphology.

1. Embryonic cells called **neural crest** migrate to distant sites in the embryo and give rise some parts of the skeleton, e. g. parts of the cranium.
2. **Pronounced cephalization**: well-developed brain, eyes, ears all concentrated in the head.
3. **Cranium** encloses and protects the brain. Hagfishes do not have a cranium but have all other characteristics of the vertebrates. This group is very ancient and predates the development of the vertebral column and cranium. Craniate animals and hagfishes are grouped in the clade **Craniata**.
4. **Vertebral column** present; it replaces the notochord in most species.
5. Two pairs of **appendages**.
6. **Endoskeleton** made of muscle, and cartilage or bone. Muscles attached to the endoskeleton for movement.
7. A **heart** made of at least two chambers, **hemoglobin**, and **red blood cells**.

**Origin of craniates**

Fossil found in China show intermediate forms between the urochordates and vertebrates, as well as the oldest vertebrate fossil dating back to the Cambrian explosion 530 million years ago.

These organisms had some characters of craniates like a small but well formed brain, eyes and muscular segments similar to craniates.

*“The description by Shu et al. (1999) of* Myllokunmingia *from the Lower Cambrian of South China is generally what one might have expected of a very primitive craniate. The surprising exception is the probable presence of paired fin folds, as well as a definite dorsal fin. None of the fins have detectable radials. The state of preservation is also insufficient to state whether* Myllokunmingia *had eyes, a single heart, an anterior notochord, or even a brain, so that the exact position of this fossil is uncertain. Shu describes it as a vertebrate, but the evidence is unclear. Perhaps it is better treated as a pre-vertebrate craniate…”*

**References:** [Janvier (1999)](http://www.palaeos.com/Vertebrates/Units/020Craniata/References.html#Janvier1999); [Shu et al. (1999)](http://www.palaeos.com/Vertebrates/Units/020Craniata/References.html#Shuetal1999); [Zimmer (2000)](http://www.palaeos.com/Vertebrates/Units/020Craniata/References.html#Zimmer2000).

<http://www.palaeos.com/Vertebrates/Units/020Craniata/100.html#Craniata>

Other interesting sites about Myllokunmingia and Haikouella.

<http://www.palaeos.com/Vertebrates/Units/010Chordata/010.200.html#Haikouella>

<http://www.nature.com/cgi-taf/DynaPage.taf?file=/nature/journal/v402/n6761/full/402518a0_r.html>

**Class Myxini (hagfishes)**

The hagfishes are most primitive living vertebrates diverging from the vertebrate lineage about 530 million years ago during the early Cambrian. .

1. The Myxini are unique among living chordates in that they have a **partial cranium** (skull), but **no vertebrae**, and so they are not truly vertebrates.
2. Their skeleton is composed of **cartilage**, and lacks vertebrae. They have a **notochord** extending the length of their body.
3. Hagfish also **lack jaws**.
4. They have **four pairs of tentacles** surrounding the mouth, and have large ventral glands that produce slime.
5. Their **eyes are reduced**.
6. They are considered vertebrates only if vertebrates are equated with the Craniata: neural crest, paired sensory organs of the head (cephalization), brain and skull (cranium).

There are about 30 species all of them marine, bottom-dwelling scavengers.

<http://tolweb.org/tree?group=Hyperotreti>

<http://tolweb.org/tree?group=Hyperotreti&contgroup=Craniata>

<http://www.ucmp.berkeley.edu/vertebrates/basalfish/myxini.html>

**VERTEBRATES**

Vertebrates are craniates that have a backbone.

A lineage of craniates evolved into vertebrates during the Cambrian.

Vertebrates became active predators because of their more complex nervous system and skeleton.

**DERIVED CHARACTERS OF THE VERTEBRATES**

1. After branching off from other craniates, they underwent another gene duplication involving a group of **transcription factor genes called the *Dlx* family**.

* These genes are involved in the development of more complex nervous and skeletal systems.

1. The **vertebral column** consists of some cartilaginous prongs along the notochord in a few vertebrates, but in the majority, the vertebral column consists of vertebrae encasing the nerve cord.

* The vertebral column replaced the notochord in its mechanical role.

1. **Dorsal, ventral and anal fins** stiffened by rays developed in aquatic vertebrates.

Morphology, fossil and molecular evidence are used to subdivide the vertebrates.

Lampreys and hagfishes lack jaws and are grouped in the Superclass **Agnatha**.

All other vertebrates have hinged jaws and are called Superclass **Gnathostomata**.

The gnathostomes are subdivided into cartilaginous fishes and three groups of bony fishes. All four groups have paired fins for swimming.

All other gnathostomes are **tetrapods**, that is, they have four appendages used in locomotion.

Amphibians lack amniotic sac in their eggs. All other groups are called **amniotes**, after the amniotic sac found in the egg or in the embryonic development.

**JAWLESS VERTEBRATES**

The agnathans represent an ancient lineage that predates the development of paired fins, teeth and ossification of bones.

**Class Petromyzontida**

Lampreys are the oldest living lineage of vertebrates.

1. There are about 35 species of lamprey living in fresh and salt water.
2. Lampreys are **anadromous**. That is, they are hatched and grow in fresh water, migrate to the ocean to mature, and then return to fresh water to spawn.
3. Unlike hagfishes, with which they were once classified, lampreys have a **complete cranium** or braincase.
4. Their **skeleton** is entirely of **cartilage** lacking **collagen**; it consists of a stiff protein matrix.
5. The **notochord** persists in the adult and is surrounded by cartilage. Pairs of cartilaginous projections extend upwards and partially surround the nerve cord. These are considered **rudimentary true vertebrae**.
6. Uniquely among living vertebrates, lampreys also have a **single "nostril"** on the dorsal side of the head -- a feature they share with various fossil jawless fish, which had a similar opening.
7. They lack paired appendages.
8. The larva is a suspension feeder. Some species are parasitic on fish. Other species feed only as larvae, when they reach sexual maturity, they reproduce and die.

Cambrian fossils support the hypothesis that brain and braincase evolved first followed by the vertebral column, with jaws, ossified skeleton, and paired appendages evolving later.

<http://www.biology.ucok.edu/AnimalBiology/Chordata/Vertebrata/Agnatha/Agnatha.html>

**Extinct jawless vertebrates**

Jawless vertebrates were more common in the past than in the present.

**Conodonts** represent an ancient lineage of vertebrates dating back 510 million years.

* Their cone-shaped teeth were ossified.
* They also had myomeres present, fin rays present, notochord present, probably a post-anal tail, and possibly a dorsal hollow nerve cord.
* Their eyes were very large.
* All are extinct but considered more advanced than hagfishes, which still survive to this day.

**Ostracoderms** thrived between 450 and 375 million years ago, from the Ordovician to the late Devonian.

* They had bony external shields that covered the head and most of the trunk.
* They were small, less than 50 cm (20 inches) long.
* Their internal skeleton was made of cartilage.
* They lacked paired fins but some has side flaps that helped in steering.
* They were probably bottom dwellers that sucked up mud or suspension feeders that trapped their food in the gills.
* They declined rapidly in the Devonian after true fishes evolved and became extinct by the end of the Devonian.
* Recent research considers some member of this group to be more closely related to jawed fish than to other ostracoderms.

**Origins of bones and teeth**.

The vertebrate skeleton evolved initially as a structure of unmineralized cartilage.

Mineralization of the skeleton took place after the lampreys diverged from other vertebrates.

What initiated the process of mineralization in vertebrates?

* Mineralization may have been associated with the transition to new feeding mechanisms.
* The earliest known mineralized structures in vertebrates were conodont dental elements. Mineralization began in the mouth according to Donoghue.
* The armor seen in later jawless vertebrates was derived from dental mineralization.
* Only in more derived vertebrates did the endoskeleton begin to mineralize, starting with the skull.

**GNATHOSTOMES**

During the Silurian (439-409 mya) and the early Devonian (409-390 mya) the agnathans were replaced by the **gnathostomes**, the jawed fishes.

**Evolutionary developments**:

* Jaws allowed a more efficient carnivorous behavior by grabbing, tearing and chewing. Flat-opposed teeth can grind hard food.
* Paired fins became more developed.

Jaws allowed these fishes to exploit food sources that were unavailable to agnathans.

Development of the jaw, a hypothesis.

* Anterior pharyngeal gill arches previously used for filter feeding became the mandible and palatoquadrate bone.
* The hyoid arch was incorporated to support the hinged of the jaw.
* The remaining gill slits were no longer required for suspension feeding and remained as the major sites of respiratory gas exchange.

**DERIVED CHARACTERS OF THE GNATHOSTOMES*.***

1. Gnathostomes share other derived characters besides **jaws**.
2. The common ancestors of all gnathostomes underwent an additional duplication of the ***Hox* genes**, so that the single cluster present in early chordates became four.
3. Other **gene clusters also duplicated**, allowing further complexity in the development of gnathostome embryos.
4. The gnathostome **forebrain is enlarged**, in association with enhanced senses of vision and smell.
5. The **lateral line system** evolved as a row of microscopic organs sensitive to vibrations in the surrounding water.
6. The common ancestor of living gnathostomes had a mineralized axial skeleton, shoulder girdle, and two sets of paired appendages.

7. Gnathostome jaws and paired fins were **major evolutionary breakthroughs**.

Jaws, with the help of teeth, enable the animal to grip food items firmly and slice them up.

Paired fins, along with the tail, enable fishes to maneuver accurately while swimming.

With these adaptations, many fish species were active predators, allowing for the diversification of both lifestyles and nutrient sources.

Gnathostomes appeared in the fossil record in the mid-Ordovician period, about 470 million years ago, and steadily diversified.

**Fossil gnathostomes**

The earliest gnathostomes appear in the fossil record in the Late Ordovician, ~ 505-440 m.y.a., an extinct lineage of armored vertebrates called **placoderms.**

Most placoderms were less than a meter long, although some giants were more than 10 m long.

In many Placoderms, the head and front part of the body (thorax) was covered by a strong armor of rigid and fused bony plates.

Other forms developed scales and small bony plates. The endoskeleton was made of cartilage or mineralized cartilage.

The Placoderms had paired pectoral and pelvic fins. The fins were weak. Giants of 9 meters length are known, others were only a few centimeters long.

Another group of jawed vertebrates called **acanthodians** radiated in the Devonian.

Acanthodians were closely related to the ancestors of osteichthyans (ray-finned and lobe-finned fishes).

They possess features found in both sharks and bony fishes. They are like early bony fishes in possessing ganoid-like scales and a partially ossified internal skeleton. Certain aspects of the jaw appear to be more like those of bony fishes than sharks, but the bony fin spines and certain aspects of the gill apparatus would seem to favor relationships with early sharks.

An ancestor common to placoderms and acanthodians may have given rise to modern sharks and bony fishes about 425 to 450 million years ago.

Both placoderms and acanthodians disappeared by the beginning of the Carboniferous period, 360 million years ago.

There are two **extant groups** of aquatic gnathostomes:

* **Chondrichthyes** (cartilaginous fish), e. g. sharks, rays, chimeras.
* **Osteichthyes** (bony fish): ray-finned fish, lobed finned fish and lungfishes.

**CLASS CHONDRICHTHYES** Cartilaginous fishes

The class **Chondrichthyes,** sharks and their relatives, includes some of the biggest and most successful vertebrate predators in the oceans.

Probably originated in salt water.

Skin with **placoid scales**; their structure is similar to that of teeth.

The notochord is replaced by vertebrae.

Chondrichthyes have relatively flexible **endoskeletons of cartilage** rather than bone.

* In most species, parts of the skeleton are impregnated by calcium.

Conodonts and armored, jawless fishes show that mineralization of the vertebrate skeleton had begun before the chondrichthyan lineage branched off from other vertebrates.

* Traces of bone can be found in living chondrichthyes, in their scales, at the base of their teeth and (in some sharks) in a thin layer on the surface of their vertebrae.
* The loss of bone in chondrichthyes is a derived condition, which emerged after they diverged from other gnathostomes.

There are about 750 extant species, almost all in the subclass of sharks and rays, with a few dozen species in a second subclass of chimaeras or ratfishes.

* All have well-developed jaws and paired fins.

The streamlined bodies of most sharks enable them to be swift, but not maneuverable, swimmers.

* Powerful axial muscles power undulations of the body and caudal fin to drive the fish forward.
* The dorsal fins provide stabilization.
* While some buoyancy is provided by low-density oils in the large liver, the flow of water over the pectoral and pelvic fins also provides lift to keep the animal suspended in the water column.

Continual swimming also ensures that water flows into the mouth and out through the gills.

* Some sharks and many skates and rays spend much time resting on the seafloor, using the muscles of their jaws and pharynx to pump water over the gills.

Most sharks are carnivores that swallow their prey whole or use their powerful jaws and sharp teeth to tear flesh from animals too large to swallow.

* In contrast, the largest sharks and rays are suspension feeders that consume plankton.
* Sharks have several rows of teeth that gradually move to the front of the mouth as old teeth are lost.
* Within the intestine of a shark is a **spiral valve,** a corkscrew-shaped ridge that increases surface area and prolongs the passage of food along the short digestive tract.

Acute senses are adaptations that go along with the active, carnivorous lifestyle of sharks.

* Sharks have sharp vision but cannot distinguish colors.
* Their acute olfactory sense (smelling) occurs in a pair of nostrils that do not function in breathing.
* Sharks can detect electrical fields, including those generated by the muscle contractions of nearby prey, through patches of specialized skin pores.
* The lateral line system, a row of microscopic organs sensitive to pressure changes, can detect low-frequency vibrations.
* In sharks, the whole body transmits sound to the hearing organs of the inner ear.

Shark eggs are fertilized internally.

Males transfer sperm via claspers on their pelvic fins to the reproductive tract of the female.

* **Oviparous** sharks encase their eggs in protective cases and lay them outside the mother’s body.
* These hatch months later as juveniles.
* **Ovoviviparous** sharks retain fertilized eggs in the oviduct.
* The embryo completes development in the uterus, nourished by the egg yolk.
* A few sharks are **viviparous,** providing nutrients through a placenta to the developing offspring.
* The reproductive track of the shark opens along with the excretory and digestive systems into a chamber called the **cloaca**, which in turn opens to the outside.

Rays are closely related to sharks, but they have adopted a very different lifestyle.

* Most rays are flattened bottom dwellers that crush mollusks and crustaceans in their jaws.
* The enlarged pectoral fins of rays are used like wings to propel the animal through the water.
* The tail of many rays is whiplike and may bear venomous barbs for defense against threats.

Chondrichthyans have changed little in more than 300 million years.

* They are severely threatened by overfishing.
* In 2003, researchers reported that shark stocks in the northwest Atlantic declined 75% in 15 years.

**CLASS OSTEICHTHYES** Bony fishes

Probably originated in fresh water.

The vast majority of bony fishes belong to a clade of gnathostomes called the Osteichthyes (meaning “bony fish”).

Systematists today include tetrapods with bony fish in Osteichthyes, which otherwise would be paraphyletic.

Skin usually with overlapping **dermal scales**, some fish without scales.

The skin of bony fishes is often covered with thin, flattened bony scales that differ in structure from the tooth-like scales of sharks.

Glands in the skin secrete mucus that reduces drag in swimming.

Skeleton with many vertebrae replace the notochord.

Nearly all bony fishes have an ossified endoskeleton with a hard matrix of **calcium phosphate**.

* It is not clear when the shift to a bony skeleton took place during gnathostome evolution.

Bony fishes breathe by drawing water over four or five pairs of gills located in chambers covered by a protective flap, the **operculum.**

* Water is drawn into the mouth, through the pharynx, and out between the gills by movements of the operculum and muscles surrounding the gill chambers.

Most fishes have an internal, air-filled sac, the **swim bladder.**

* The positive buoyancy provided by air counters the negative buoyancy of the tissues, enabling many fishes to be neutrally buoyant and remain suspended in the water.
* The swim bladder evolved from balloonlike lungs that may have been used to breathe air when dissolved oxygen levels were low in stagnant shallow waters.

Like sharks, aquatic osteichthyes have a lateral line system, which is evident as a row of tiny pits in the skin on either side of the body.

The reproduction of aquatic osteichthyes varies.

* Most species are oviparous, reproducing by external fertilization after the female sheds large numbers of small eggs.
* Internal fertilization and birthing characterize other species.

**Ray-fin fishes**

The most familiar families of fishes belong to the **ray-finned fishes,** members of class Actinopterygii.

* This class includes bass, trout, perch, tuna, and herring.
* In this group, the fins are supported by long, flexible rays.
* The fins may be modified for maneuvering, defense, and other functions.

Bony fishes, including the ray-finned fishes, probably evolved in fresh water and then spread to the seas during their long history.

* Many species of ray-finned fishes returned to fresh water at some point in their evolution.
* Some ray-finned fishes, such as salmon, make a round-trip from fresh water to seawater and back to fresh water during their life cycle.

**Lobed-fin fishes**

Ray-finned fishes evolved during the Devonian period, along with the **lobe-finned** fishes (Sarcopterygii).

The key derived character in **lobe-fins** is the presence of muscular pectoral and pelvic fins supported by extensions of the bony skeleton.

* Many Devonian lobe-fins were large, bottom dwellers that may have used their paired, muscular fins to “walk” along the bottom.
* By the end of the Devonian period, lobe-fin diversity was dwindling.

Today, only three lineages survive.

* One lineage, the coelacanths (class Actinistia) probably originated as freshwater animals with lungs, but others shifted to the ocean, including the only living genus, *Latimeria*.
* The second lineage of living lobe-fins is represented by three genera of lungfishes (class Dipnoi), which live today in the Southern Hemisphere.
  + They generally inhabit stagnant ponds and swamps.
  + They can gulp air into lungs connected to the pharynx of the digestive tract to provide oxygen for metabolism.
  + Lungfishes also have gills, which are the main organs for gas exchange in Australian lungfishes.
  + When ponds shrink during the dry season, some lungfishes can burrow into the mud and estivate.
  + There are three extant species of lungfishes.
* The third lineage of lobe-fins that survives today is far more diverse than coelacanths or lungfishes.

There are about 30,000 species of bony fishes.

Many zoologists recognize now three classes instead of one class:

* Class Actinopterigii: ray-finned fishes, those most familiar to us.
* Class Actinistia: lobed-finned fishes, like the coelacanth.
* Class Dipnoi: lungfishes.

**TETRAPODS ARE GNATHOSTOMES WITH LIMBS AND FEET**

During the Devonian, plants and arthropods already inhabit the land and had diversified.

Plants living near water created new habitats in which lobed-fin and lungfishes evolved.

During the mid-Devonian, the tetrapods adapted to life on land and gave rise to terrestrial vertebrates, including humans.

Descendants of the bony fishes moved onto land during the Devonian (408-380 m.y.a.), about 360 million years ago.

This is one of the most significant events in vertebrate history.

Lobed-finned fishes are very similar to those that moved onto land.

*"The current thinking (as expressed mainly by Ahlberg, Clack and Coates) is that the tetrapod limb evolved primarily in an aquatic environment, more precisely, in very shallow lagoonal or lacustrine waters. That "urlimb", whether it was pentadactyl, hexadactyl, heptadactyl (and so on) evolved to facilitate propulsion in that shallow water, to "row" on the bottom, or to "propel" the animal when launching an attack (most early tetrapods or near tetrapods were highly predacious animals). In second instance, this limbs were also quite decent for locomotion on the land but they evolved in first instance for other purposes..."*

Ref: [www.cmnh.org/dinoarch/1998Jun/msg00804.html](file:///C:\Documents%20and%20Settings\gérald\Bureau\www.cmnh.org\dinoarch\1998Jun\msg00804.html) - 7k; Pieter.Depuydt@rug.ac.be

**DERIVED CHARACTERISTICS OF TETRAPODS**

This is the name given to any four legged vertebrate animal and those descended from them, that is, those that have lost legs: snakes, glass lizards, caecilians, etc.

The most significant character of **tetrapods** is the four limbs, which allow them to support their weight on land.

* The feet of tetrapods have digits that allow them to transmit muscle-generated forces to the ground when they walk.

With the move to land, the bones of the pelvic girdle (to which the hind legs are attached) became fused to the backbone, permitting forces generated by the hind legs against the ground to be transferred to the rest of the body.

Living tetrapods do not have pharyngeal gill slits.

* The ears are adapted to the detection of airborne sounds.

The Devonian coastal wetlands were home to a wide range of lobe-fins. Those that entered shallow, oxygen-poor water could use their lungs to breathe air.

Some species likely used their stout fins to move across the muddy bottom.

* At the water’s edge, leglike appendages were probably better equipment than fins for paddling and crawling through the dense vegetation in shallow water.
* The tetrapod body plan was thus a modification of a preexisting body plan.

In one lineage of lobe-fins, the fins became progressively more limb-like, while the rest of the body retained adaptations for aquatic life.

* The earliest amphibians on record are *Acanthostega* and *Ichthyostega*.
* *Acanthostega* was an early tetrapod that was ill suited for life on land. It has internal gills and led an aquatic life.
* Fossils of *Acanthostega* from 365 million years ago had bony gill supports and rays in its tail to support propulsion in water, but it also had fully formed legs, ankles, and digits.
* *Acanthostega* is representative of a period of vertebrate evolution when adaptations for shallow water allowed certain fishes to make a gradual transition to the terrestrial side of the water’s edge.

A great diversity of tetrapods emerged during the Carboniferous period.

* Judging from the morphology and location of the fossils, most of these early tetrapods remained tied to water.

**THE ORIGIN OF TETRAPODS**

**AMPHIBIANS**

***Class Amphibia: Salamanders, frogs, and caecilians are the three extant amphibian orders.***

Today the **amphibians** (class Amphibia) are represented by about 4,800 species of salamanders (order Urodela, “tailed ones”), frogs (order Anura, “tail-less ones”), and caecilians (order Apoda, “legless ones”).

Some of the 500 species of urodeles are entirely aquatic, but others live on land as adults or throughout life.

* On land, most salamanders walk with a side-to-side bending of the body that may resemble the swagger of the early terrestrial tetrapods.

The 4,200 species of anurans are more specialized than urodeles for moving on land.

* Adult frogs use powerful legs to hop along the terrain.
* Frogs nab insects by flicking out their sticky tongues, which are attached to the front of the mouth.

Anurans may be camouflaged or secrete a distasteful, even poisonous, mucus from skin glands.

* Many poisonous species are brightly colored, perhaps to warn predators who associate the coloration with danger.

Apodans, the caecilians (about 150 species), are legless and nearly blind.

* The reduction of legs evolved secondarily from a legged ancestor.

Superficially resembling earthworms, most species burrow in moist forest soil in the tropics.

* A few South American species live in freshwater ponds and streams.

*Amphibian* means “two lives,” a reference to the metamorphosis of many frogs from an aquatic stage, the tadpole, to the terrestrial adult.

* Tadpoles are usually aquatic herbivores with gills and a lateral line system, and they swim by undulating their tails.
* During metamorphosis, the tadpole develops legs, the lateral line disappears, and lungs replace gills.
* Adult frogs are carnivorous hunters.

Many amphibians do not live a dualistic—aquatic and terrestrial—life.

* There are some strictly aquatic and some strictly terrestrial: frogs, salamanders, and caecilians.
* The larvae of salamanders and caecilians look like adults and are also carnivorous.

Paedomorphosis, the retention of some larval features in a sexually mature adult, is common among some groups of salamanders.

* For example, the mudpuppy (*Necturus*) retains gills and other larval features when sexually mature.

Most amphibians retain close ties with water and are most abundant in damp habitats.

* Those adapted to drier habitats spend much of their time in burrows or under moist leaves where the humidity is higher.
* Most amphibians rely heavily on their moist skin to carry out gas exchange with the environment.
  + Some terrestrial species lack lungs entirely and breathe exclusively through their skin and oral cavity.

Amphibian eggs lack a shell and dehydrate quickly in dry air.

* Most species have external fertilization, with eggs shed in ponds or swamps or at least in moist environments.
* Some species lay vast numbers of eggs in temporary pools where mortality is high.
* Others display various types of parental care and lay relatively few eggs.
  + In some species, males or females may house eggs on the back, in the mouth, or even in the stomach.
  + Some species are ovoviviparous or viviparous, retaining the developing eggs in the female reproductive tract until released as juveniles.

Many amphibians display complex and diverse social behavior, especially during the breeding season.

* Then many male frogs fill the air with their mating calls as they defend breeding territories or attract females.
* In some terrestrial species, migrations to specific breeding sites may involve vocal communication, celestial navigation, or chemical signaling.

For the past 25 years, zoologists have been documenting a rapid and alarming decline in amphibian populations throughout the world.

Several causes that have been proposed include habitat degradation, the spread of a pathogen (a chytrid fungus), and acid precipitation.

* Acid precipitation is damaging to amphibians because of their dependence on wet places for completion of their life cycles.

**AMNIOTES**

**Amniotes have amniotic eggs**

The **amniote** clade consists of the mammals and reptiles (including birds).

The evolution of amniotes from an amphibian ancestor involved many adaptations for terrestrial living.

The **amniotic egg** is the major derived character of the clade.

**DERIVED CHARACTERS OF AMNIOTES**

***Evolution of the amniotic egg expanded the success of vertebrates on land.***

Inside the shell of the amniotic egg are several **extraembryonic membranes** that function in gas exchange, waste storage, and the transfer of stored nutrients to the embryo.

* The amniotic egg is named for one of these membranes, the amnion, which encloses a fluid-filled “private pond” that bathes the embryo and acts as a hydraulic shock absorber.

The amniotic eggs enabled terrestrial vertebrates to complete their life cycles entirely on land.

* In contrast to the shell-less eggs of amphibians, the amniotic eggs of most amniotes have a shell that retains water and can be laid in a dry place.
* The calcareous shells of bird eggs are inflexible, while the leathery eggs of many reptiles are flexible.
* Most mammals have dispensed with the shell.
  + The embryo implants in the wall of the uterus and obtains its nutrition from the mother.

Amniotes acquired other adaptations to terrestrial life, including less-permeable skin and the increasing use of the rib cage to ventilate the lungs.

Amniotes adopt a more elevated stance than earlier tetrapods and living amphibians.

**Early amniotes**

The most recent common ancestor of living amphibians and amniotes lived about 340 million years ago, in the early Carboniferous period.

* No fossils of amniotic eggs have been found from that time.

Early amniotes lived in drier environments than did earlier tetrapods.

Some were herbivores, with grinding teeth. Others were large and predatory.

**REPTILES**

***The reptile clade includes birds.***

The **reptile** clade includes tuatara, lizards, snakes, turtles, crocodilians, and birds, as well as extinct groups such as dinosaurs.

Reptiles have several adaptations for terrestrial life not generally found in amphibians.

* Scales containing the protein keratin waterproof the skin, preventing dehydration in dry air.
  + Crocodiles, which are adapted to water, have evolved more permeable scales called scutes.
* Reptiles obtain all their oxygen with lungs, not through their dry skin.
* As an exception, many turtles can use the moist surfaces of their cloaca for

gas exchange.

Most reptiles lay shelled amniotic eggs on land.

* Fertilization occurs internally, before the shell is secreted as the egg passes through the female’s reproductive tract.
* Some species of lizards and snakes are viviparous, with their extraembryonic membranes forming a placenta that enables the embryo to obtain nutrients from its mother.

Nonbird reptiles are sometimes labeled “cold-blooded” because they do not use their metabolism extensively to control body temperature.

* However, many nonbird reptiles regulate their body temperature behaviorally by basking in the sun when cool and seeking shade when hot.

Because they absorb external heat rather than generating much of their own, nonbird reptiles are more appropriately called **ectotherms.**

* One advantage of this strategy is that an ectothermic reptile can survive on less than 10% of the calories required by a mammal of equivalent size.

The reptile clade is not entirely ectothermic.

* Birds are **endothermic,** capable of keeping the body warm through metabolism.

**The origin and evolutionary radiation of reptiles**

The oldest reptilian fossils date back to the Carboniferous period, about 300 million years ago.

The first major group of reptiles to emerge was the **parareptiles,** large, stocky, quadrupedal herbivores.

* Some parareptiles had dermal plates on their skin, which may have provided defense against predators.

Parareptiles died out 200 million years ago, at the end of the Triassic period.

As parareptiles were dwindling, an equally ancient clade of reptiles, the **diapsids,** was diversifying.

* The most obvious derived character of diapsids is a pair of holes on each side of the skull, behind the eye socket.

The diapsids are composed of two main lineages.

* One, the **lepidosaurs,** includes lizards, snakes, and tuataras.
  + This lineage also produced a number of marine reptiles including plesiosaurs and ichthyosaurs.
* The **archosaurs** include crocodilians, and the extinct pterosaurs and dinosaurs.

**Pterosaurs,** which originated in the late Triassic, were the first flying tetrapods.

* The pterosaur wing is formed from a bristle-covered membrane of skin that stretched between the hind leg and the tip of an elongated finger.
* Well-preserved fossils show the presence of muscles, blood vessels, and nerves in the wing membrane, suggesting that pterosaurs could dynamically adjust their membranes to assist their flight.

**Dinosaurs** were an extremely diverse group varying in body shape, size, and habitat.

* There were two main dinosaur lineages: the ornithischians, which were mostly herbivorous, and the saurischians, which included both long-necked giant herbivores and bipedal carnivorous **theropods**.
  + Theropods included the famous *Tyrannosaurus rex* as well as the ancestors of birds.

There is increasing evidence that many dinosaurs were agile; fast moving; and, in some species, social.

* Paleontologists have discovered signs of parental care among dinosaurs.

There is continuing debate about whether dinosaurs were **endothermic,** capable of keeping their body warm through metabolism.

* Some experts are skeptical.
* In the warm, consistent Mesozoic climate, behavioral adaptations may have been sufficient for maintaining a suitable body temperature for terrestrial dinosaurs.
* Also, the low surface-to-volume ratios would have reduced the effects of daily fluctuations in air temperature on the animal’s internal temperature.
* Some anatomical evidence supports the hypothesis that at least some dinosaurs were endotherms.
  + Paleontologists have found fossils of dinosaurs in both Antarctica and the Arctic, although the climate in those areas was milder during the Mesozoic than today.
* The dinosaur that gave rise to birds was certainly endothermic, as are all birds.

By the end of the Cretaceous, all dinosaurs (except birds) became extinct.

* It is uncertain whether dinosaurs were declining before they were finished off by an asteroid or comet impact.

**Lepidosaurs**

Lepidosaurs are represented by two living lineages.

One lineage includes the tuatara, two species of lizard-like reptiles found only on 30 islands off the coast of New Zealand.

* Tuatara relatives lived at least 220 million years ago, when they thrived on every continent well into the Cretaceous period.

The other major living lineage of lepidosaurs is the squamates (lizards and snakes).

Lizards are the most numerous and diverse reptiles alive today.

* Most are relatively small, but they range in length from 16 mm to 3 m.

Snakes are legless lepidosaurs that evolved from lizards closely related to the Komodo dragon.

It was once thought that snakes were descendents of lizards that adapted to a burrowing lifestyle through the loss of limbs.

* However, recently discovered fossils of aquatic snakes with complete hind legs suggest that snakes likely evolved in water and then recolonized land.
* Some species of snakes retain vestigial pelvic and limb bones, providing evidence of their ancestry.

Snakes are carnivorous, and a number of adaptations aid them in hunting and eating prey.

* Snakes have acute chemical sensors and are sensitive to ground vibrations.
* The flicking tongue fans odors toward olfactory organs on the roof of the mouth.
* Heat-detecting organs of pit vipers, including rattlesnakes, enable these night hunters to locate warm animals.
* Some poisonous snakes inject their venom through a pair of sharp, hollow or grooved teeth.
* Loosely articulated jaws enable most snakes to swallow prey larger than the diameter of the snake itself.

**Turtles**

Turtles are the most distinctive group of reptiles alive today.

All turtles have a boxlike shell made up of upper and lower shields that are fused to the vertebrae, clavicles, and ribs.

The earliest fossils of turtles are 220 million years old, with fully developed shells.

* The origin of the turtle shell remains a puzzle.
* Some paleontologists suggest that turtle shells evolved from the dermal shells of parareptiles.
* Other studies link turtles to archosaurs or lepidosaurs.
* There are two separate branches of turtles that have independently evolved mechanisms to retract their heads.
* Turtles live in a variety of environments, from deserts to ponds to the sea.

**Alligators and crocodiles**

Crocodiles and alligators (crocodilians) are among the largest living reptiles.

* They spend most of their time in water, breathing air through upturned nostrils.
* Crocodilians are confined to the tropics and subtropics.

**BIRDS**

There are 8,600 species of birds in the world.

***Birds evolved as feathered dinosaurs.***

Like crocodilians, birds are archosaurs, but highly specialized for flight.

* In addition to amniotic eggs and scales, modern birds have feathers and other distinctive flight equipment.

**DERIVED CHARACTERS OF BIRDS**

Almost every part of a typical bird’s anatomy is modified in some way to reduce weight and enhance flight.

* One adaptation to reduce weight is the absence of some organs.
  + For instance, females have only one ovary.
* Modern birds are toothless and grind their food in a muscular gizzard near the stomach.

The skeletons of birds have several adaptations that make them light and flexible, but strong.

* The bones are air-filled and honeycombed to reduce weight without sacrificing much strength.

A bird’s feathers have a hollow, air-filled shaft that is light and strong.

* Feathers are made of beta-keratin, a protein similar to the keratin of reptile scales.

The shape and arrangement of feathers forms wings into airfoils.

Power for flapping the wings comes from contractions of the pectoral muscles, anchored to a keel on the sternum.

The evolution of flight required radical alteration in body form but provides many benefits.

* Flight enhances hunting and scavenging.
* It enables many birds to exploit flying insects, an abundant, highly nutritious food resource.
* Flight provides a ready escape from earthbound predators.
* It enables many birds to migrate great distances to exploit different food resources and seasonal breeding areas.

Flying requires a great expenditure of energy with an active metabolism.

* Birds are endothermic, using their own metabolic heat to maintain a constant body temperature.
* Feathers and, in some species, a layer of fat provide insulation.
* Efficient respiratory and circulatory systems with a four-chambered heart keep tissues well supplied with oxygen and nutrients.
* The lungs have tiny tubes leading to and from elastic air sacs that help dissipate heat and reduce body density.
* Birds have excellent vision and coordination, supported by well-developed areas of the brain.
* The large brains of birds (proportionately larger than those of reptiles or amphibians) support very complex behavior.
* During the breeding season, birds engage in elaborate courtship rituals.
  + This culminates in copulation, contact between the mates’ vents, and the openings to their cloacae.
  + After eggs are laid, the avian embryo is kept warm through brooding by the mother, father, or both, depending on the species.

**Origin of birds**

Cladistic analyses of fossilized skeletons support the hypothesis that the closest reptilian ancestors of birds were **theropods.**

In the late 1990s, Chinese paleontologists unearthed a treasure trove of feathered theropods that are shedding light on bird origins.

* These fossils suggest that feathers evolved long before feathered flight, possibly for insulation or courtship.

Theropods may have evolved powered flight by one of two possible routes.

1. Small ground-running dinosaurs chasing prey or evading predation may have used feathers to gain extra lift as they jumped into the air.
2. Dinosaurs could have glided from trees, aided by feathers.

The most famous Mesozoic bird is *Archaeopteryx*, known from fossils from a German limestone quarry.

* This ancient bird lived about 150 million years ago, during the late Jurassic period.
* *Archaeopteryx* had clawed forelimbs, teeth, and a long tail containing vertebrae.
* Without its feathers, *Archaeopteryx* would probably be classified as a theropod dinosaur.
* Its skeletal anatomy indicates that it was a weak flyer, perhaps a tree-dwelling glider.

**Living birds**

Neornithes, the clade that includes 28 orders of living birds, arose after the Cretaceous-Tertiary boundary, 65 million years ago.

Most birds can fly, but Neornithes includes a few flightless birds, the **ratites,** which lack both a breastbone and large pectoral muscles.

* The ratites include the ostrich, kiwi, and emu.

The penguins make up the flightless order Sphenisciformes.

* They have powerful pectoral muscles, which they use in swimming.

The demands of flight have rendered the general form of all flying birds similar to one another.

* The beak of birds is very adaptable, taking on a great variety of shapes for different diets.

**MAMMALS**

Mammals are amniotes that have **hair** and produce **milk**.

Mammals diversified extensively in the wake of the Cretaceous extinctions.

**DERIVED CHARACTERS OF MAMMALS**

**Mammals** have a number of derived traits.

* All mammalian mothers use mammary glands to nourish their babies with milk, a balanced diet rich in fats, sugars, proteins, minerals, and vitamins.
* All mammals also have hair, made of keratin.
* Hair and a layer of fat under the skin retain metabolic heat, contributing to endothermy in mammals.
* Endothermy is supported by an active metabolism, made possible by efficient respiration and circulation.
  + Adaptations include a muscular diaphragm and a four-chambered heart.

Mammals generally have larger brains than other vertebrates of equivalent size.

* Many species are capable of learning.
* The relatively long period of parental care extends the time for offspring to learn important survival skills by observing their parents.

Feeding adaptations of the jaws and teeth are other important mammalian traits.

* Unlike the uniform conical teeth of most reptiles, the teeth of mammals come in a variety of shapes and sizes adapted for processing many kinds of foods.
* During the evolution of mammals from reptiles, two bones formerly in the jaw joint were incorporated into the mammalian ear and the jaw joint was remodeled.

**Early evolution of mammals**

Mammals belong to a group of amniotes known as **synapsids.**

* Synapsids have a temporal fenestra behind the eye socket on each side of the skull.

Synapsids evolved into large herbivores and carnivores during the Permian period.

Mammal-like synapsids emerged by the end of the Triassic, 200 million years ago.

* These animals were not mammals, but they were small and likely hairy, fed on insects at night, and had a higher metabolism that other synapsids.
* They likely laid eggs.

The first true mammals arose in the Jurassic periods.

* Early mammals diversified into a number of lineages, all about the size of a shrew.

During the Mesozoic, mammals coexisted with dinosaurs and underwent a great adaptive radiation in the Cenozoic in the wake of the Cretaceous extinctions.

* Modern mammals are split into three groups: monotremes (egg-laying mammals), marsupials (mammals with pouches), and eutherian (placental) mammals.

**Monotremes**

Monotremes are found in Australia and New Guinea.

* There is one species of platypus and two of echidnas.

**Monotremes**—the platypuses and the echidnas—are the only living mammals that lay eggs.

* The reptile-like egg contains enough yolk to nourish the developing embryo.

Monotremes have hair, and females produce milk in specialized glands.

* After hatching, the baby sucks milk from the mother’s fur because she lacks nipples.

**Marsupials**

**Marsupials** include opossums, kangaroos, bandicoots, and koalas.

Marsupials and eutherians share derived characters not found among monotremes.

In contrast to monotremes, marsupials have a higher metabolic rate, have nipples that produce milk, and give birth to live young.

The embryo develops inside the uterus of the female’s reproductive tract.

The lining of the uterus and the extraembryonic membranes that arise from the embryo form a **placenta**.

* The **placenta** is a structure in which nutrients diffuse into the embryo from the mother’s blood.

A marsupial is born very early in development and, in most species, completes its embryonic development while nursing within a maternal pouch, the **marsupium**.

* In most species, the tiny offspring climbs from the exit of the female’s reproductive tract to the mother’s pouch.

Marsupials existed worldwide throughout the Mesozoic area but now are restricted to Australia and the Americas.

* In Australia, marsupials have radiated and filled niches occupied by eutherian mammals in other parts of the world.
  + Through convergent evolution, these diverse marsupials resemble eutherian mammals that occupy similar ecological roles.

While marsupial mammals diversified throughout the Tertiary in South America and Australia, the placental mammals began an adaptive radiation on the northern continents.

* Australia’s isolation facilitated the diversification and survival of its marsupial fauna.
* Invasions of placental mammals from North America impacted the marsupial fauna of South America about 12 million years ago and then again about 3 million years ago when the continents were connected by the Isthmus of Panama.
* This mammalian biogeography is an example of the interplay between biological and geological evolution.

**Eutherians**

Eutherians are also called **placental mammals**.

* Their placenta is more complex than those of the marsupials.

Compared to marsupials, **eutherian mammals** (placentals) have a longer period of pregnancy.

* Young eutherians complete their embryonic development within the uterus, joined to the mother by the placenta.
* Eutherians are commonly called placental mammals because their placentas are more complex than those of marsupials and provide a more intimate and long-lasting association between mother and young.

**PRIMATES**

**Primates and the Evolution of *Homo sapiens***

Primate evolution provides a context for understanding human origins.

Primates include lemurs, monkeys, and apes.

**DERIVED CHARACTERS OF PRIMATES**

1. Primates have large brains and short jaws.
2. Their eyes are forward-looking.
3. Most primates have hands and feet adapted for grasping.
4. Relative to other mammals, they have large brains and short jaws.
5. They have flat nails on their digits, rather than narrow claws.
6. Primates also have relatively well-developed parental care and relatively complex social behavior.
7. The earliest primates were probably tree dwellers, shaped by natural selection for arboreal life.

* The grasping hands and feet of primates are adaptations for hanging on to tree branches.
  + All modern primates, except *Homo*, have a big toe that is widely separated from the other toes.
  + The thumb is relatively mobile and separate from the fingers in *all* primates, but a *fully* **opposable thumb** is found only in anthropoid primates.
  + The unique dexterity of humans, aided by distinctive bone structure at the thumb base, represents descent with modification from ancestral hands adapted for life in the trees.

8. Other primate features also originated as adaptations for tree dwelling.

* The overlapping fields of vision of the two eyes enhance depth perception, an obvious advantage when brachiating.
* Excellent hand-eye coordination is also important for arboreal maneuvering.

**Living primates**

Primates are divided into two subgroups.

* The Prosimii **(prosimians)** probably resemble early arboreal primates and include the lemurs of Madagascar and the lorises, pottos, and tarsiers of tropical Africa and southern Asia.
* The Anthropoidea **(anthropoids)** include monkeys, apes, and humans.

The oldest known anthropoid fossils, from about 45 million years ago, support the hypothesis that tarsiers are the prosimians most closely related to anthropoids.

By the Oligocene, monkeys were established in Africa, Asia, and South America.

* The Old World and New World monkeys underwent separate adaptive radiations.
* All New World monkeys are arboreal, but Old World monkeys include arboreal and ground-dwelling species.
* Most monkeys in both groups are diurnal, and usually live in bands held together by social behavior.

In addition to monkeys, the anthropoid suborder also includes four genera of apes: *Hylobates* (gibbons), *Pongo* (orangutans), *Gorilla* (gorillas), and *Pan* (chimpanzees and bonobos).

* Modern apes are confined exclusively to the tropical regions of the Old World.
* They evolved from Old World monkeys about 20–25 million years ago.

With the exception of gibbons, modern apes are larger than monkeys, with relatively long

arms and short legs and no tails.

* Only gibbons and orangutans are primarily arboreal.

Social organization varies among the genera, with gorillas and chimpanzees being highly social.

* Apes have relatively larger brains than monkeys, and their behavior is more flexible.

**Humans are bipedal hominoids.**

In the continuity of life spanning more than 3.5 billion years, humans and apes have shared ancestry for all but the past few million years.

**DERIVED CHARACTERS OF HUMANS**

Human evolution is marked by the evolution of several major features.

* Humans stand upright and walk on two legs.
* Humans have a much larger brain than other hominoids and are capable of language, symbolic thought, and tool use.
* Humans have reduced jawbones and muscles and a shorter digestive tract.
* Human and chimpanzee genomes are 99% identical.
  + Scientists are comparing the genomes of humans and chimpanzees to investigate the 1% difference.

**The earliest hominids**

**Paleoanthropology** is the study of human origins and evolution.

**Paleoanthropology** is the study of human origins and evolution focused on the time when humans and chimpanzees diverged from a common ancestor.

* Anthropoids = monkeys, apes and human.
* Hominoids = apes and humans.
* Hominids = a species that is closer to humans than to chimp.

Different human features evolved at different rates (**mosaic evolution**).

Paleoanthropologists have found fossils of 20 species of extinct hominoids that are more closely related to humans than to chimpanzees.

* These species are known as **hominids.**

The oldest hominid is *Sahelanthropus tchandensis*, which lived 7 million years ago.

* *Sahelanthropus* and other early hominids shared some of the derived characters of humans.
* They had reduced canine teeth and relatively flat faces.
* They were more upright and bipedal than other hominoids.

While early hominids were becoming bipedal, their brains remained small—about 400 to 450 cm3 in volume.

* Early hominids were small in stature, with relatively large teeth and a protruding lower jaw.

Avoid three common sources of confusion:

1. First, our ancestors were not chimpanzees or any other modern apes.
   * Chimpanzees and humans represent two divergent branches of the hominoid tree that evolved from a common ancestor that was neither a chimpanzee nor a human.
2. Second, human evolution did not occur as a ladder with a series of steps leading directly from an ancestral hominoid to *Homo sapiens*.
   * If human evolution is a parade, then many splinter groups traveled down dead ends, and several different human species coexisted.
   * Human phylogeny is more like a multibranched bush with our species as the tip of the only surviving twig.
3. Third, the various human characteristics, such as upright posture and an enlarged brain, did not evolve in unison.
   * Different features evolved at different rates, called **mosaic evolution.**
   * Our pedigree includes ancestors who walked upright but had brains much less developed than ours.

* After dismissing some of the folklore on human evolution, we must admit that many questions about our own ancestry remain.

**Australopiths**

Hominid diversity increased dramatically between 4 and 2 million years ago.

The various pre-*Homo* hominids are classified in the genus *Australopithecus* (“southern ape”) and are known as australopiths.

* The first australopith, *A. africanus*, was discovered in 1924 by Raymond Dart in a quarry in South Africa.
  + From this and other skeletons, it became clear that *A. africanus* probably walked fully erect and had humanlike hands and teeth.
  + However, the brain was only about one-third the size of a modern human’s brain.

In 1974, a new fossil, about 40% complete, was discovered in the Afar region of Ethiopia.

* This fossil, nicknamed “Lucy,” was described as a new species, *A. afarensis*.

Based on this fossil and other discoveries, this species had a brain the size of a chimpanzee, a prognathous jaw, longer arms (for some level of arboreal locomotion), and sexual dimorphism more apelike than human.

* However, the pelvis and skull bones and fossil tracks showed that *A. afarensis* walked bipedally.
* Two lineages appeared after *A. afarensis*: the “robust” australopithecines with sturdy skulls and powerful jaws and teeth for grinding and chewing hard, tough foods; and the “gracile” australopithecines with lighter feeding equipment adapted for softer foods.

**Bipedalism**

Combining evidence from the earliest hominids with the fossil record of australopiths makes it possible to consider hypotheses about trends in hominid evolution.

Why did hominids become bipedal?

* Our anthropoid ancestors of 30–35 million years ago were tree dwelling.
* Twenty million years ago, the forests contracted as the climate became drier.
* The result was an increased savanna with few trees.
* For decades, paleontologists thought that bipedalism was an adaptation to life on the savanna.
* All early hominids show indications of bipedalism, but they lived in forests and open woodlands, not savanna.
* An alternate hypothesis is that bipedalism allowed hominids to reach low-hanging fruits.
* About 1.9 million years ago, hominids living in arid environments walked long distances on two legs.

**Tool use**

The manufacture and use of complex tools is a derived human character.

* When and why did tool use arise in the human lineage?
* Other hominoids are capable of sophisticated tool use.
  + Orangutans can fashion probes from sticks for retrieving insects from their nests.
  + Chimps use rocks to smash open food and put leaves on their feet to walk over thorns.
* The oldest generally accepted evidence of tool use is 2.5-million-year-old cut marks on animal bones found in Ethiopia.
  + The australopith fossils near the site had relatively small brains.
  + Perhaps tool use originated before large hominid brains evolved.

**Early Homo**

The earliest fossils that anthropologists place in our genus, *Homo*, are classified as *Homo habilis*.

* These fossils range in age from 2.4 to 1.6 million years old.
* This species had less prognathic jaws and larger brains (about 600–750 cm3) than australopiths.
* In some cases, anthropologists have found sharp stone tools with these fossils, indicating that some hominids had started to use their brains and hands to fashion tools.

Fossils from 1.9 to 1.6 million years ago are recognized as a distinct species, *Homo ergaster*.

* *H. ergaster* had a larger brain than *Homo habilis*, as well as long slender legs well adapted for long-distance walking.
* This species lived in more-arid environments and was associated with more-sophisticated tool use.
* Its reduced teeth suggest that it might have been able to cook or mash its food before eating it.

Specimens of early *Homo* show reduced sexual dimorphism, a trend that continued with our

species.

* Sexual dimorphism is reduced in pair-bonding species.
* Male and female *Homo ergaster* may have engaged in more pair-bonding than earlier hominids, perhaps in order to provide long-term biparental care of babies.

Some paleontologists still think that *Homo ergaster* were merely early specimens of *Homo erectus.*

*Homo erectus* was the first hominid species to migrate out of Africa, colonizing Asia and Europe.

They lived from about 1.8 million to 500,000 years ago.

Fossils from Asia are known by such names as “Beijing man” and “Java Man.”

In Europe, Neanderthals arose from an earlier species, *Homo heidelbergensis,* which arose in Africa about 600,000 years ago and spread to Europe.

**Neanderthals**

In 1856, miners discovered some human fossils in a cave in the Neander Valley in Germany.

The term Neanderthal is now used for humans who lived throughout Europe from about 200,000 to 30,000 years ago.

* Fossilized skulls indicate that Neanderthals had brains as large as ours, though somewhat different in shape.
* They made hunting tools from stone and wood.
* Neanderthals were generally more heavily built than modern humans; they had a thick prominent brow.

Neanderthals apparently went extinct about 30,000 years ago, contributing little to the gene pool of modern humans.

Evidence of the extinction of Neanderthal can be found in their DNA.

* Scientists have extracted DNA from four fossil Neanderthals living at different times and places in Europe.
* Neanderthals appear to have descended form Homo heidelbergensis that originated in Africa about 600,000 years ago and then dispersed to Europe and the Middle East.
  + All Neanderthals formed a clade, while modern Europeans were more closely related to modern Africans and Asians.

**Homo sapiens**

It is now clear that the ancestors of humans originated in Africa.

Older species, perhaps H. ergaster or H. erectus, gave rise to newer species, such as H. heidelbergensis and eventually H. sapiens.

In 2003, researchers in Ethiopia found 160,000-year-old fossils of *Homo sapiens*, the oldest members of our species.

* These early humans were slender and lacked brow ridges.

Evidence suggests that all living humans are more closely related to each other than to Neanderthals.

Europeans and Asians share a relatively recent common ancestor and many African lineages branched off from more ancient positions on the human family tree.

* This is supported by analysis of mDNA and Y chromosomes of various populations.

These findings strongly suggest that all living humans arose from Africa and migrated from there 50,000 years ago.

* The oldest fossils of H. sapiens outside Africa are about 50,000 years old. .

Our ancestors emerged in one or more waves, spreading into Asia, then Europe, and Australia.

* The date of the first arrival of humans in the New World is generally accepted to be about 15,000 years old.

The rapid expansion of our species may have been spurred by the evolution of human cognition.

* Neanderthals produced sophisticated tools, but had little creativity or capacity for symbolic thought.

In 2002, researchers found 77,000-year-old art from South Africa.

By 36,000, humans were producing spectacular cave paintings.

Symbolic thought may have emerged along with full-blown human language, raising the reproductive fitness of humans by allowing them to construct new tools and teach others how to build them.

Population pressure may have driven humans to migrate into Asia and then Europe.

In 2002, geneticists found that *FOXP2*, a gene essential for human language, experienced intense natural selection after the ancestors of humans and chimps diverged.

* Comparisons of flanking regions of the gene suggest that most changes took place within the past 200,000 years.
* The evolutionary change in *FOXP2* may be the first genetic clue about how our own species came to be.